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# Final Scientific Report

# Comparative neurophysiology of vision

GIUSEPPE MORUZZI
INSTITUTE OF PHYSIOLOGY - UNIVERSITY OF PISA (ITALY)

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## I. - Introduction

This annual report covers the investigations carried out on the project «Comparative neurophysiology of vision» supported by the Contract AF EOAR 61 (052) - 830.

From September 15, 1965 to September 14, 1966 the following themes were investigated:

1) Visual control of flashing in the fireflies (Magni).

2) Evidence of presynaptic inhibition in the lateral geniculate body following reticular stimulation (Kahn, Magni and Pillai).

3 Presynaptic inhibition in the lateral geniculate body with regard to the problem of reciprocal binocular interaction (Kawamura and Marchiafava; Marchiafava).

4) Receptor and neural responses in the cat's retina (Maffei and Poppele).

5) Temporal and spatial relations in retinal units (Gestri, Maffei and Petracchi).

6) Surgical immobilization of eye and pupil (Berlucchi, Munson and Rizzolatti).

## II. - The research workers

Dr. F. Magni is assistant professor of the Institute of Physiology and acting professor of General Physiology.

Dr. P. L. Marchiafava is assistant professor of the Institute of Physiology.

Drs. G. Berlucchi and L. Maffei are research associates of the Consiglio Nazionale delle Ricerche (CNR).

Dr. G. Rizzolatti had a fellowship of the Ministero della Pubblica Istruzione.

Drs. G. Gestri and D. Petracchi are research associates of the Institute of Physics of the University of Pisa.

Drs. N. Kahn, from the Columbia University, J. B. Munson, from the University of Rochester and R.E. Poppele, from the University of Minnesota, had fellowship of the P. H. S. Dr. Poppele will spend at Pisa also the year 1966-67. Dr. V. Pillai was IBRO-Unesco fellow while Dr. H. Kawamura had a CNR fellowship.

## III. - Results

1. *Visual control of flashing in fireflies* - Magni's experiments, which were summarized in the previous annual Report, had shown that steady photic stimulation of strong intensity inhibits spontaneous flashing in the firefly *Luciola italica*, whereas facilitation of both strength and frequency of spontaneous flashes occurs when steady illumination is low in intensity (C: 7). The work carried out by Dr. Magni (A: 9) during this year was mainly concerned with the neural mechanisms underlying the effects of steady illumination, particularly with regard to the nature of the light-induced inhibition of flashing.

Male specimens were fastened to a small board and the flashes were recorded by means of a photomultipler, the output of which was led to a cathode rays oscillograph (C.R.O.). A projector lamp, focused onto the eyes of the animal, produced photic stimuli, the duration of which could be controlled by means of an electromagnetically driven shutter. The intensity of illumination was changed by means of calibrated neutral filters. Bipolar platinum electrodes, inserted on the midline of the thorax, were used to stimulate the ventral cord with square pulses, whose intensity, duration and repetition rate could be varied at will. The electrical responses of the abdominal ganglia were recorded on CRO by means of a copper wire, 100 μ in diameter, insulated to the tip, which was inserted through a small opening in the cuticle, the indifferent electrode having been placed on the abdomen.

The following results have been obtained:

1) In the *intact* fireflies, electrical stimulation of the ventral cord at 300/sec produces clear cut facilitation of *spontaneous* flashing, whereas stimulation at the rate of 30/sec produces inhibition of the spontaneous flashing. The threshold strenght was always lower for facilitatory than for inhibitory responses.

II) There is no spontaneous flashing in the *decapitated* firefly, in confirmation of older findigs (see B: 2). Direct stimulation of the lantern with single electrical pulses elicits flashes (see B: 3 and 4 for ref.), which can be facilitated and inhibited by stimulation of the ventral cord at 30/sec and 300/sec respectively. These results were not contaminated by spread of currents, as shown by control experiments.

III) Bursts of impulses can be recorded from the abdominal ganglia of *intact* fireflies in correspondence of each spontaneous flash. The recorded potentials are probably due to volleys descending to the lantern, since they are always recorded before the flashing, the interval being about 150 msec; they are not abolished, moreover, by destroying the lantern.

IV) When the eyes of the *intact* firefly are stimulated by strong steady light both nerve volleys and flashing disappear. By reducing the intensity of the steady illumination, a critical level may be found which will produce inhibition of flashing, without affecting the nerve volleys. When steady illumination is low both the rate of flashes and of neural volleys is increased.

These experiments suggest that central and peripheral mechanisms play a rôle in the inhibition of spontaneous flashing by steady illumination. The stimulation experiments summarized in II) would suggest, moreover, that also the facilitation of flashing may be due in part to peripheral mechanisms, However the evidence is less strong than for inhibition.

These investigations will be extended next Spring.

2) *Depolarization of optic fiber endings in the lateral geniculate body.* - Experiments summarized in the previous report (see C: 1,2) have shown that stimulation of the mesencephalic reticular formation enhances the excitability of the intrageniculate endings of the optic tract fibers. Similar results have been obtained from the lateral geniculate body (L.G.B.) following electric stimulation of discrete cortical areas (B: 6, 8). Following reticular stimulation slow potentials can be recorded from the peripheral stump of the optic nerve (C: 1), which are similar in shape to the dorsal root potentials of the spinal cord (see B: 5 for ref.).

Kahn, Magni and Pillai (A: 3) have performed a series of experiments in order to ascertain whether the depolarization of the optic fibers is produced by some active mechanism or is passively determined by a potential field due to activity of structures in or around the L.G.B. The experiments were performed in unanesthetized midpontine pretrigeminal cats. Stimulating electrodes were placed in the optic chiasm and in the mesencephalic reticular formation. Glass micropipettes (diameter approx. 0.1 μ, resistance 30 MΩ), filled with 3M KCL, were inserted in the lateral geniculate body, for intracellular recording.

Fibers of the optic tract could be penetrated at the level of L.G.B. and were identified according to the following criteria: a) the latency of the response to chiasmatic stimulation was shorter than 0.5 msec; b) the response followed the stimulus even at repetition rates of 300/sec; c) no prepotentials were seen associated with the response, nor were spontaneously occurring postsynaptic potentials observed.

When the reticular formation was stimulated with brief trains of shocks, the membrane of the intrageniculate optic fibers was depolarized. The depolarization had a latency of 30-40 msec from the beginning of the stimulation, reached a peak in 50-60 msec and declined to zero after more than 100 msec. When the microelectrode was withdrawn to a position just outside the fiber, the potential field was found to be less than the internally recorded depolarization.

The recorded fibers could be classified as « on », « off », or « on-off » according to their responses to diffuse light stimulation of the eyes. The reticular stimulation was found to be equally effective on all three types of fiber.

It is concluded from these findings that the depolarization of the intrageniculate endings of the optic fiber is produced by an active mechanism, which is likely to be similar in kind to that postulated for presynaptic inhibition. The physiological significance of presynaptic inhibition in the visual system will be further investigated.

3) *Reciprocal binocular interaction at the level of the lateral geniculate body.* - A possible role of presynaptic inhibition in the neural mechanisms underlying reciprocal binocular interaction is suggested by the experiments of Marchiafava (A: 10).

Working on unanesthetized midpontine pretrigeminal cats Kawamura and Marchiafava (A: 4) had shown that a single conditioning shock (CS) delivered to one optic nerve enhances the excitability of the intrageniculate endings of optic fibers arising from the contralateral retina. This increase in excitability was demonstrated, following Wall's principle (see previous report, p. 5, for ref.), by leading from the opposite optic nerve the antidromic response to a test shock (TS) applied to L.G.B., ipsilaterally to the recorded side.

The same CS also caused a slow negative potential which could be recorded from the contralateral optic nerve stump. Both the enhancement of the antidromic response and the slow potential may be regarded as suggestive evidence (see B: 5) that presynaptic inhibition can be elicited reflexly by afferent optic volleys.

Section of the optic tract, ipsilaterally to the side where the CS was applied, did not prevent the enhancement of the antidromic response, nor the appearance of the slow negative potential, an observation suggesting that the conditioning volley reached the tested L.G.B. through crossed optic fibers. Hence an inhibitory interaction may occur between optic volleys coursing along fibers which converge upon the same L.G.B. from two hemiretinas subserving the same visual field.

The experiments suggested that a reflexly induced presynaptic inhibition, occurring at L.G.B. levels, might be involved in the mechanism of reciprocal binocular interaction. They could by not be regarded, however, as a demonstration of such an assumption, since there was no proof that the interrelation between the two retinas was strictly specific in nature nor that the effect could be reproduced by using light as a conditioning stimulus. These proofs have been provided by later experiments of Marchiafava (A: 10).

A first group of experiments was carried out by applying the CS to and recording the antidromic response from the exposed internal surfaces of the two retinas. This technique permitted to demonstrate that the effect was strictly specific, since *a*) for given localization of the geniculate electrode the antidromic response to the TS could be recorded only from a limited area (about 2 $mm^2$) of the ipsilateral retina and *b*) the CS was effective in increasing the antidromic response only when it was applied to the corresponding area of the contralateral retina. The specificity of the effect

was so marked that conditioning stimulation of neighboring retinal districts, even within the same retinal quadrant, was completely ineffective.

In a second group of experiments the CS was represented by the illumination of a small retinal area (about 200 μ in diameter). The enhancement of the antidromic response was obtained only when the natural stimulus fell onto the retinal area corresponding to the contralateral retinal area from which the antidromic response was recorded.

This reciprocal inhibition might provide a mechanism to explain binocular retinal rivalry. In given experimental conditions the impulses coming from one eye might block presynaptically, at geniculate level, the volleys arising from the 'non-dominant' retina. The perceptual alternation of the two monocular images which by their different shapes and contours prevent the single binocular vision might be due to the reciprocal organization of this inhibition.

4) *Receptor and neural responses in the cat's retina.* - Maffei and Poppele (A: 5, 6) have recorded the electroretinographic responses from the cat's retina during dark adaptation. The experiments were performed on the intact retina and after chronic photocoagulation of the retinal artery, following a technique introduced by other investigators (B: 1) in order to inactivate the neural elements of the retina and to record only the receptor response. A study of the b wave of the normal retina and of the receptor response suggest that there is a neural stage in dark adaptation (see B: 5) that occurs at the level of the inner nuclear layer level.

Maffei and Poppele (A: 7, 8) have also carried out, mainly by means of sinusoidally modulated light, a linear analysis of both the receptor response and the normal E.R.G. Under resonable assumptions a comparison between the frequency response of the receptors and of the ERG shows that the neural part compensates some attenuation in the high frequency response occurring at receptor level.

5) *Temporal and spatial relations in retinal units.* - Gestri, Maffei and Petracchi (A: 2) have carried out a statistical analysis of retinal unit discharge in darkness, steady light, and under sinusoidally modulated light. They have found that the interval distri-

bution is an invariant when referred to the average discharge. They have also studied relations between different units detected by the same microelectrode and distinguishable on the basis of their different amplitudes. Study of the correlation coefficient between adjacent units has revealed in all the analyzed cases a statistical independence between the events of a unit and those of the adjacent one, both in darkness and under steady light stimulation.

6) *Surgical immobilization of eye and pupil.* - In studies of visually-evoked brain potentials in freely moving animals, a major technical difficulty is represented by the instability of the testing stimulus. Eye movements, variations in pupil size etc. are factors which can introduce undesired changes of photic stimulation. Berlucchi, Munson and Rizzolatti (A: 1) have devised a simple method for cutting the motor nerves to the eye and the pupil in the cat. The oculomotor and trochlear nerves are cut in the fossa cranialis media, after lifting the temporal pole of the hemisphere. The abducens nerve is cut at its emergency from the pons; the approach is through the auditory bulla and the basiocciput. A binocular dissecting microscope is used throughout for the finer steps of the surgery. Paralysis of the m. dilatator of the pupil is obtained by cutting the cervical sympathetic trunk in the neck, either pre- or postganglionically. Stimuli delivered to a paralized eye by means of a neon bulb attached to a corneal lens remain constant despite gross bodily movements. The method is suitable for the study of photically evoked potentials in waking and sleeping animals.

## BIBLIOGRAPHY

A) *Pubblications supported by the present Contract.*

1) Berlucchi, G., Munson, J.B. and Rizzolatti, G. - Surgical immobilization of the eye and pupil, permitting stable photic stimulation of freely moving cats. - *EEG clin. Neurophysiol.* (in press).

2) Gestri, G., Maffei L., and Petracchi, D. - Temporal and spatial relationships in retinal units. *Kybernetic* (in press).

3) Kahn, N., Magni, F. and Pillai, V. - Depolarization of optic fiber endings in the lateral geniculate body. *Arch. ital. Biol.* (in press).

4) KAWAMURA, H. and MARCHIAFAVA, P.L. - Aumento d'eccitabilità delle terminazioni centrali del nervo ottico prodotto dalla stimolazione del nervo controlaterale. *Rend. Accad. naz. Lincei, Cl. Sci. fis. mat., nat.*, Ser. VIII, *40*: 119-121, 1966.

5) MAFFEI, L. and POPPELE, R.E. - Electrophysiological evidence for a neural stage in dark adaptation. *Experientia* (in press).

6) MAFFEI, L. and POPPELE, R.E. - Neural stage in dark adaptation. *Arch. ital. Biol.* (in press).

7) MAFFEI, L. and POPPELE, R.E. - Linear electroretinographic responses to low-level illumination (in preparation).

8) MAFFEI, L. and POPPELE, R.E. - Receptor and neural components of retinal functions (in preparation).

9) MAGNI, F. - (In preparation).

10) MARCHIAFAVA, P.L. - Binocular reciprocal interaction upon optic fiber endings in the lateral geniculate nucleus of the cat. *Brain Res.*, *2*: 188-192, 1966.

B) *Other publications quoted in the progress report.*

1) BROWN, K.T. and WATANABE, K. - Isolation and identification of a receptor potential from the pure cone fovea of the monkey retina. *Nature, 193*: 958-960, 1962.

2) BUCK, B.J. - The anatomy and physiology of the light organ in fireflies. *Ann. N.Y. Acad. Sci., 49*: 397-482, 1948.

3) BUCK, B.J. and CASE, J.F. - Control of flashing in fireflies. I - The lantern as a neuroeffector organ. *Biol. Bull., 121*: 234-256, 1961.

4) BUCK, B.J., CASE, J.F. and HANSOW, F.E. Jr. - Control of flashing in fireflies. III - Peripheral excitation. *Biol. Bull., 125*: 251-269, 1963.

5) ECCLES, J.C., MAGNI, F. and WILLIS, W.D. - Depolarization of central terminals of group I afferent fibers from muscle. *J. Physiol., 160*: 62-93, 1962.

6) IWAMA, K., SAKAKURA, H. and KASAMATSU, T. - Presynaptic inhibition in the lateral geniculate body induced by stimulation of the cerebral cortex. *Jap. J. Physiol., 15*: 310-322, 1965.

7) RUSHTON, W.A.H. - Dark adaptation and the regeneration of rhodopsin. *J. Physiol., 156*: 166-178, 1961.

8) SUSUKI, H. and KATO, E. - Cortically induced presynaptic inhibition in cat's lateral geniculate body. *Tohoku J. exp. Med., 86*: 277-289, 1965.

C) *Works quoted in the previous reports which have been published during the last year.*

1) ANGEL, A., MAGNI, F. and STRATA, P. - Evidence for presynaptic inhibition in the lateral geniculate body. *Nature, 208*: 495-496, 1965.

2) ANGEL, A., MAGNI, F. and STRATA, P. - Excitability of intrageniculate optic tract fibres after reticular stimulation in the midpontine pretrigeminal cat. *Arch. ital. Biol., 103*: 668-693, 1965.

3) HUGHES, G.W. and MAFFEI, L. - Retinal ganglion cell response to sinusoidal light stimulation. *J. Neurophysiol., 25*: 333-352, 1966.

4) MAFFEI, L., MORUZZI, G. and RIZZOLATTI, G. - Influences of sleep and wakefulness on the response of lateral geniculate units to sinewave photic stimulation. *Arch. ital. Biol., 103*: 596-608, 1965.

5) MAFFEI, L. and RIZZOLATTI, G. - Effect of synchronized sleep on the responses of lateral geniculate units to flashes of light. *Arch. ital. Biol., 103*: 609-622, 1965.

6) MAFFEI, L. and RIZZOLATTI, G. - Unit responses of the lateral geniculate body to light flashes during wakefulness and synchronized sleep. *Experientia, 21*: 533, 1965.

7) MAGNI, F. - Effetti della stimolazione luminosa sul lampeggiamento delle lucciole (*Luciola italica*). *Boll. Soc. ital. Biol. sper.* (in press).

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**The results of the following ~~theme of~~ investigation are reported:**

1. **Visual control of flashing in the fireflies.**
2. **Evidence of presynaptic inhibition in the lateral geniculate body following reticular stimulation.**
3. **Presynaptic inhibition in the lateral geniculate body with regard to the problem of reciprocal binocular interaction.**
4. **Receptor and neural responses in the cat's retina.**
5. **Temporal and spatial relations in retinal units.**
6. **Surgical immobilization of eye and pupil.**

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